Heritability of Drought Resistance Traits and Correlation of Drought Resistance and Agronomic Traits in Peanut

P. Songsri, S. Jogloy,* T. Kesmala, N. Vorasoot, C. Akkasaeng, A. Patanothai, and C. C. Holbrook

ABSTRACT

Inheritance of traits is important for developing effective breeding schemes for improving desired traits. The aims of this study were to estimate the heritabilities (h^2) of drought resistance traits and the genotypic (r_G) and phenotypic (r_P) correlations between drought resistance traits and agronomic traits, and to examine the relationships between drought resistance traits under stressed and nonstressed conditions. The 140 lines in the $F_{4:7}$ and $F_{4:8}$ generations from four peanut (*Arachis hypogaea* L.) crosses were tested under field capacity (FC) and two-thirds available soil water (2/3 AW) in two field experiments. Data were recorded for specific leaf area (SLA), SPAD chlorophyll meter reading (SCMR), and biomass, pod yield, harvest index, number of mature pods per plant, seed per pod, and seed size. The h^2 for biomass, pod yield, DTI (drought tolerance index) (pod yield), DTI (biomass), HI, SLA, and SCMR were high for all tested crosses (0.54–0.98). The r_G (−0.61 and −0.66) and r_P (−0.61 and −0.66) between SLA and SCMR were strong and negative under 2/3 AW and FC. Under 2/3 AW conditions, SCMR was positively correlated with pod yield and seed size. Compared to SLA, SCMR had higher r_G and r_P with pod yield, biomass, and other agronomics traits. Significant correlations between FC and 2/3 AW conditions were found for pod yield, biomass, SCMR, and SLA, indicating that these traits could be selected under FC or 2/3 AW conditions. SPAD chlorophyll meter reading, which is easy to measure, is potentially useful as a selection trait for drought resistance because of high h^2 and positive correlation with pod yield and agronomic traits.

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Abbreviations: 2/3 AW, two-thirds available soil water; BIO, biomass; DAS, days after sowing; DTI, drought tolerance index; E, environment; FC, field capacity; G, genotype; HI, harvest index; PY, pod yield; SCMR, SPAD chlorophyll meter reading; SLA, specific leaf area; TE, transpiration efficiency; WUE, water use efficiency; Y, year.

Drought is the major abiotic constraint affecting peanut (*Arachis hypogaea* L.) productivity and quality worldwide. Two-thirds of the global production occurs in rain-fed regions of the semi-arid tropics where rainfall is generally erratic and insufficient, causing unpredictable drought stress, the most important constraint for peanut production (Wright and Nageswara Rao, 1994; Reddy et al., 2003). Even peanut grown under irrigation may experience drought because of limited water supply or because irrigation water is applied in amounts at frequencies less than optimal for plant growth. Improving water access and management are practically difficult since water is a scarce resource. Therefore, breeding for drought resistance is an important strategy in alleviating the problem and offers the best long-term solution. Selection of segregating populations under stress conditions has been a standard approach for developing cultivars with improved stress tolerance. While direct selection for yield under stressed conditions can be effective, the limitations of this approach are high resource investment and poor repeatability of the results due to the large genotype ×

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environment (G×E) interaction that results in slow breeding progress (Wright et al., 1996).

More rapid progress may be achieved by using physiological traits (Nigam et al., 2005) such as harvest index (HI) or water use efficiency (WUE), specific leaf area (SLA), and SPAD chlorophyll meter reading (SCMR). Both SLA and SCMR have been used as surrogate traits for WUE (Wright et al., 1994; Nageswara Rao and Wright, 1994; Sheshshayee et al., 2006; Nigam et al., 2005). In a biological model, yield is explained to be a function of water transpired, WUE, and HI (ratio of economic yield to total biomass produced) (Passioura, 1986). Water use efficiency, defined as total biomass production per unit of water transpired, is not an easy trait to measure and, therefore, is not practical for use in large-scale breeding programs for improving drought tolerance.

Water use efficiency is negatively correlated with leaf carbon isotopic composition (Δ) in a range of crop species, including peanut (Farquhar et al., 1982; Hubick et al., 1986; Wright et al., 1988, 1994). While measurement of Δ is rapid, it is an expensive technique and may not be feasible in large segregating breeding populations, particularly in developing countries. Specific leaf area, the ratio of leaf area to leaf dry weight, is negatively related to leaf thickness and Δ and hence WUE, over a wide range of cultivars and environments in peanut (Wright et al., 1994; Nageswara Rao and Wright, 1994). Significant and high correlations between SLA and ribulose 1-5 bisphosphate carboxylase (Rubisco) (Nageswara Rao et al., 1995) suggested that photosynthetic capacity per unit leaf area is the major factor contributing to variation in WUE in peanut. There are a few published reports suggesting the predominant role of additive gene effects in SLA inheritance (Nigam et al., 2001; Surihan et al., 2005). Heritability estimation of water transpired, transpiration efficiency (TE), and HI has been reported that varied between crosses and traits (Cruickshank et al., 2004).

Nageswara Rao et al. (2001) reported significant correlations among SCMR, SLA, and specific leaf nitrogen. A strong and positive relationship between SCMR and WUE was found in peanut (Sheshshayee et al., 2006). Specific leaf area and SCMR are negatively correlated (Nageswara Rao et al., 2001; Upadhyaya, 2005). Upadhyaya (2005) also reported genetic variation for SCMR in peanut.

Information on the inheritance of HI, SLA, and SCMR and the genetic correlations among these traits will be useful for planning a suitable breeding strategy for improving drought tolerance. Drought can alter the heritability estimates of these traits; therefore, genetic gain through conventional selection may be different under drought and well-watered conditions. Genetic correlations between drought resistance traits and agronomic traits have to be studied in details under drought and well-watered conditions to evaluate correlated responses to selection of drought resistance traits on agronomic traits. Objectives of this study were to estimate (i) the heritabilities of drought resistance traits, (ii) the genotypic and phenotypic correlations between drought resistance traits and agronomic traits in peanut under different water levels, and (iii) the relationship between drought resistance traits under stressed and nonstressed condition.

MATERIALS AND METHODS

Genetics Materials

Four peanut F_1 hybrids (ICGV 98308 × 'KK60-3', ICGV 98324 × KK60-3, ICGV 98308 × 'Tainan 9', and ICGV 98324 × Tainan 9) were generated from the hybridization of two drought-resistant lines (ICGV 98308 and ICGV 98324; medium-maturing [110 d to maturity] and medium-seeded type), selected for low yield reduction, with two high-yielding cultivars, KK60-3 (late-maturing [120 d to maturity] and large-seeded type) and Tainan 9 (early-maturing [100 d to maturity] and medium-seeded type). ICGV 98324 and KK 60-3 are know to have high SCMR and low SLA, ICGV 98308 has moderate SLA and moderate SCMR, and Tainan 9 has high SLA and low SCMR under both stressed and nonstressed conditions. The F_1 seeds were planted and their seeds harvested in bulk for each cross. In the F_2 and F_3 generations, two pods were kept for each plant and bulked for each cross. Line separation was performed in the F_4 generation. A total of 140 lines (35 lines for each cross) were randomly selected and multiplied in the F_5 and F_6 generation.

The 140 families from four crosses were evaluated in the $F_{4:7}$ and $F_{4:8}$ generations (F_4–derived lines in the F_7 and F_8 generations, respectively) under two soil moisture levels, field capacity (FC) and two-thirds available soil water (2/3 AW), for 2 yr in dry season 2005–2006 and 2006–2007. A split-plot design with four replications was used for both years at the Field Crop Research Station, Faculty of Agriculture Khon Kaen University, located in Khon Kaen province, Thailand (16°28′ latitude, 102°48′ longitude, 200 m above sea level) during November 2005 to March 2006, and repeated during November 2006 to April 2007. Soil type is Yasothon series (loamy sand, Ocix Paleustults), with an FC soil moisture of 11.0% and permanent wilting point of 4.6%. Two soil moisture levels, FC (11.0%) and 2/3 AW (8.8%), in 0 to 60 cm depth were assigned as main plots, and peanut lines were laid out in subplots. Each entry was planted in five row plots 3.2 m long. Spacing was 50 cm between rows and 20 cm between hills within the row.

Crop Management

Land was prepared for planting by plowing three times. Lime (625 kg ha^{-1}), phosphorus fertilizer as triple superphosphate (24.7 kg P ha^{-1}), and potassium fertilizer as potassium chloride (31.1 kg K ha^{-1}) were applied before planting. Seeds were treated with captan [3a,4,7,7a-tetrahydro-2-[(trichloromethyl)thio]-1H-isoindole-1, 3(2H)-dione] at the rate of 5 g kg^{-1} seed before planting, and seeds of the large-seeded genotypes were also treated with ethrel (2-chloroethylphosphonic acid) 48% at the rate of 2 mL L^{-1} water to break dormancy. Three to four seeds were planted per hill, and the seedlings were thinned to two plants per hill at 14 d after sowing (DAS). Rhizobium was applied to the seed by applying a water-diluted commercial peat-based inoculum of *Bradyrhizobium* (mixture of strains THA 201 and THA 205; Department of Agriculture, Ministry of Agriculture and Cooperatives, Bangkok, Thailand) on the rows of peanut plants. Weeds were controlled by an application of alachlor [2-chloro-2', 6'-diethyl-*N*-(methoxymethyl) acetanilide 48%, w v^{-1}, emulsifiable concentrate] at the rate of 3 L ha^{-1} at planting and hand weeding during the remainder of the season. Gypsum ($CaSO_4$) at the rate of 312 kg ha^{-1} was applied at 45 DAS. Carbofuran (2,3-dihydro-2, 2-dimethylbenzofuran-7-ylmethylcarbamate, 3% granular) was applied at the pod-setting stage. Pests and diseases were controlled by weekly applications of carbosulfan [2-3-dihydro-2,2-dimethylbenzofuran-7-yl (dibutylaminothio) methylcarbamate 20% w v^{-1}, water soluble concentrate] at 2.5 L ha^{-1}, methomyl [*S*-methyl-*N*-((methylcarbamoyl) oxy) thioacetimidate 40% soluble powder] at 1.0 kg ha^{-1} and carboxin [5,6-dihydro-2-methyl-1,4-oxathiine-3-carboxanilide 75% wettable powder] at 1.68 kg ha^{-1}.

A subsoil drip-irrigation system (Super Typhoon, Netafim Irrigation Equipment & Drip Systems, Israel), with a distance of 20 cm between emitters was installed with a spacing of 50 cm between drip lines at 10 cm below the soil surface midway between peanut rows and fitted with a pressure valve and water meter to ensure a uniform supply of measured amounts of water across each plot. Soil moisture was initially maintained at field capacity (102.63 mm in 60 cm depth) until 21 DAS in all treatments to support crop establishment. After 21 DAS, the 2/3 AW treatment was imposed by withholding irrigation until the soil moisture at 0 to 60 cm of soil depth was reduced to the predetermined levels of 82.57 mm at 60 cm depth. Afterward, soil moistures for the stress treatment was allowed to gradually decline until reaching the predetermined levels of 2/3 AW at 0 to 60 cm at 28 DAS, then held more or less constant until harvest. In maintaining the specified soil moisture levels, water was added to the respective plots by subsurface drip irrigation based on crop water requirement and surface evaporation, which were calculated following the methods described by Doorenbos and Pruitt (1992) and Singh and Russell (1981), respectively.

Total crop water use for each water treatment was calculated as the sum of transpiration and soil evaporation. Transpiration was calculated using the methods described by Doorenbos and Pruitt (1992):

$$ET_{crop} = ET_o K_c$$

where ET_{crop} is crop water requirement (mm d^{-1}), ET_o is evapotranspiration of a reference plant under specified conditions calculated by pan evaporation method, and K_c is the crop water requirement coefficient for peanut, which varies with genotype and growth stage (Doorenbos and Kassam, 1986). Surface evaporation (E_s) was calculated as (Singh and Russell, 1981)

$$E_s = \beta(E_o/t)$$

where E_s is soil evaporation (mm), β is light transmission coefficient measured depending on crop cover, E_o is evaporation from class A pan (mm d^{-1}), and t is days from the last irrigation or rain.

Data Collection

Weather Parameters

Weather data for both years were obtained from a meteorological station about 30 m away from the experimental site and are presented in Fig. 1.

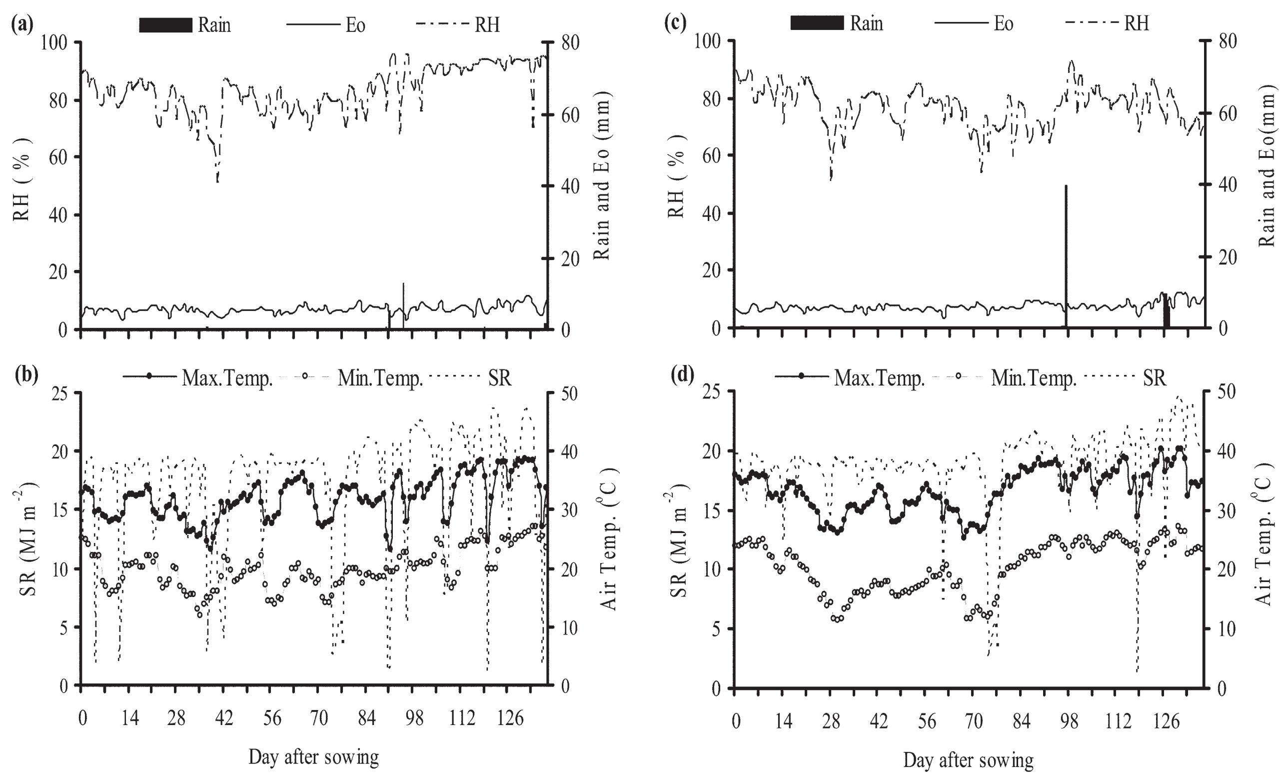

Figure 1. Rainfall, evaporation (E_O), relative humidity (RH), maximum and minimum air temperature, and solar radiation (SR) in (a, b) 2005–2006 and (c, d) 2006–2007 in Khon Kaen, Thailand.

The field trials were conducted during the dry seasons from November 2005 to March 2006 and November 2006 to April 2007. There was maximum rainfall (13.0 mm) at 95 DAS in the dry season 2005–2006, and (39 mm) at 97 DAS in the dry season 2006–2007 (Fig. 1). The seasonal mean maximum and minimum air temperature ranged between 32.0°C and 20.0°C in 2005–2006 and 33.0°C and 20.0°C in 2006–2007. Daily pan evaporation ranged from 2.8 to 9.6 mm in 2005–2006 and 2.9 to 9.8 mm in 2006–2007. Seasonal mean solar radiation was 16.7 MJ m^{-2} d^{-1} in 2005–2006 and, 18.8 MJ m^{-2} d^{-1} in 2006–2007.

Soil Moisture Status

Soil moistures were measured by the gravimetric method at planting and harvesting at the depths of 0 to 5, 25 to 30, and 55 to 60 cm. The measurement at planting was for calculating the correct amount of water to be applied to the crop, and the measurement at harvest was for calculating the water use of the crop. The soil water status was also monitored at 7-d intervals using a neutron moisture meter (Type I.H. II SER. No. N0152, Ambe Didcot Instruments Co., Abingdon, Oxon, UK). Sixteen-second neutron moisture meter readings were made at least weekly from a depth of 0.3 to 0.9 m at 0.3-m intervals.

SPAD Chlorophyll Meter Reading and Specific Leaf Area

In each plot, five plants were randomly selected to record SCMR and SLA at 52, 67, 82, and 97 DAS following the procedure described by Nageswara Rao et al. (2001). Briefly, the second fully expanded leaves were detached from the chosen plants between 8:30 and 9:30 a.m. and brought to the laboratory in zipped polythene bags for recording observations. The SPAD chlorophyll meter (Minolta SPAD-502 m, Tokyo, Japan) reading was recorded twice on each leaflet of the tetrafoliate leaf along the midrib. In recording the SCMR, care was taken to ensure that the SPAD meter sensor fully covered the leaf lamina and that interference from veins and midribs was avoided.

After recording SCMR, the leaf area of all five sampled plants was measured with a leaf area meter (LI 3100C Area Meter, LI-COR Inc., Lincoln, NE) after which leaves were dried in an oven at 80°C for at least 48 h to determine the leaf dry weight. Immediately after drying, the leaves were weighed and the SLA was derived as leaf area per unit leaf dry weight (cm^2 g^{-1}). The SLA was calculated using the following formula: SLA = leaf area (cm^2)/leaf dry weight (g).

Agronomic Traits

For each plot, three rows with 2.8 m in length (4.2 m^2) were harvested at maturity (R8) (Boote, 1982), and their pods were removed before taking fresh shoot weight in the field. A 2-kg random sample of shoots was oven-dried at 80°C for 48 h and dry weight was measured. Shoot dry matter content was then calculated and used in determining shoot dry weight for a plot. Pod yields were weighed after air drying to approximately 8% moisture content.

The number of mature pods per plant (mature pods was separated from immature pods, which were identified by dark internal pericarp color), number of seed per pod and 100 seed weight were also recorded at final harvest.

Harvest index was computed by the following formula: HI = total pod weight at the final harvest/total biomass at the final harvest.

Drought tolerance index (DTI), as suggested by Nautiyal et al. (2002), was calculated for biomass—DTI (BIO)—and pod yield—DTI (PY)—as the ratio of each parameter under stressed treatments (2/3 AW) to that under well-watered (FC) condition.

Statistical Analysis

Individual analysis of variance was performed for each year followed a split-plot design (Gomez and Gomez, 1984). Homogeneity of variance was tested for all characters and combined analysis of variance of 2-yr data was performed. Calculation procedures were conducted using MSTAT-C package (Bricker, 1989). Because water regime × genotype interaction was significant, each water regime was analyzed separately according to a randomized complete block design (Gomez and Gomez, 1984).

Estimates of broad-sense heritability for the four crosses were calculated by partitioning variance components of family mean squares to pooled environmental variance (δ^2_E) and genotypic variance (δ^2_G), and then broad-sense heritability estimates (h^2_b) were calculated as follows (Holland et al., 2003):

$$h^2_b = \delta^2_G/\delta^2_P$$

$$\delta^2_P = \delta^2_G + \delta^2_{GE}/e + \delta^2_E/re$$

where δ^2_G is genotypic variation, δ^2_P is phenotypic variation, r is number of replications, and e is number of environments. The standard error of heritability (Singh et al., 1993) for drought resistance traits was calculated to give a measure of the precision of the estimate.

Because the evaluation of heritability estimates was conducted in late generations (F_7 and F_8) of segregating materials when most genes were nearly fixed in individual genotypes, it would be expected that additive genetic variances for the traits under study were fixed through generation advance (Holland, 2001).

Phenotypic and genotypic correlations between drought resistance traits and agronomic traits were calculated following the methods of Falconer and Mackay (1996) as follows (Table 1):

$$\text{Phenotypic correlation } (r_P) = (M^\star_3 M_3)/[(M^\star_3)(M_3)]^{1/2}$$

$$\text{Genotypic correlation } (r_G) = (M^\star_3 M_3 - M^\star_2 M_2)/[(M^\star_3 - M^\star_2)(M_3 - M_2)]^{1/2}$$

Table 1. Analysis of variance of cross and cross product.

Source of variation	df	Mean square of character		MCP†	EMS†	EMCP†
		X	*Y*			
Year (Y)	Y – 1					
Rep. within Y	Y(r – 1)‡					
Families (F)	F – 1	M^*_3	M_3	M^*_3 M_3	$\delta^2_E + r\delta^2_{FE} + re\delta^2_F$	$\delta_{E^*E} + r\delta_{FE^*FE} + re\delta_{F^*F}$
F × Y	(F – l)(r – 1)	M^*_2	M_2	M^*_2 M_2	$\delta^2_E + r\delta^2_{FE}$	$\delta_{E^*E} + r\delta_{FE^*FE}$
Pooled error	Y(r – 1)(F – 1)	M^*_1	M_1	M^*_1 M_1	δ^2_E	δ_{E^*E}

†MCP, mean square of cross product; EMS, expected mean square; EMCP, expected mean square of cross product.

‡r, number of replications.

where M* is mean square of character X and M is mean square of character Y. Simple correlation was used to determine the relationship between biomass, pod yield, and drought resistance traits under well-watered and drought conditions to understand whether the performance of peanut genotypes was consistent across environments.

RESULTS AND DISCUSSION

Monitoring of Soil Moisture

Soil moisture was measured with a neutron moisture meter at 7-d intervals until harvest (Fig. 2). The results showed reasonable management of soil moistures. A clear distinction among soil moisture levels was noted at 30 cm of soil depth. Soil moistures at 90 cm depth were similar among treatments because the amount of water applied in each treatment was calculated for 0 to 60 cm. Visual wilting was observed in the 2/3 AW treatment in the afternoon.

Combined Analysis of Variance

Combined analysis of variance showed significant differences among 140 progenies ($P \leq 0.01$) for biomass production, pod yield, and the drought surrogate traits HI, SCMR, and SLA (Table 2). This indicated that genetic variation exists for these characters and, thus, that heritability could

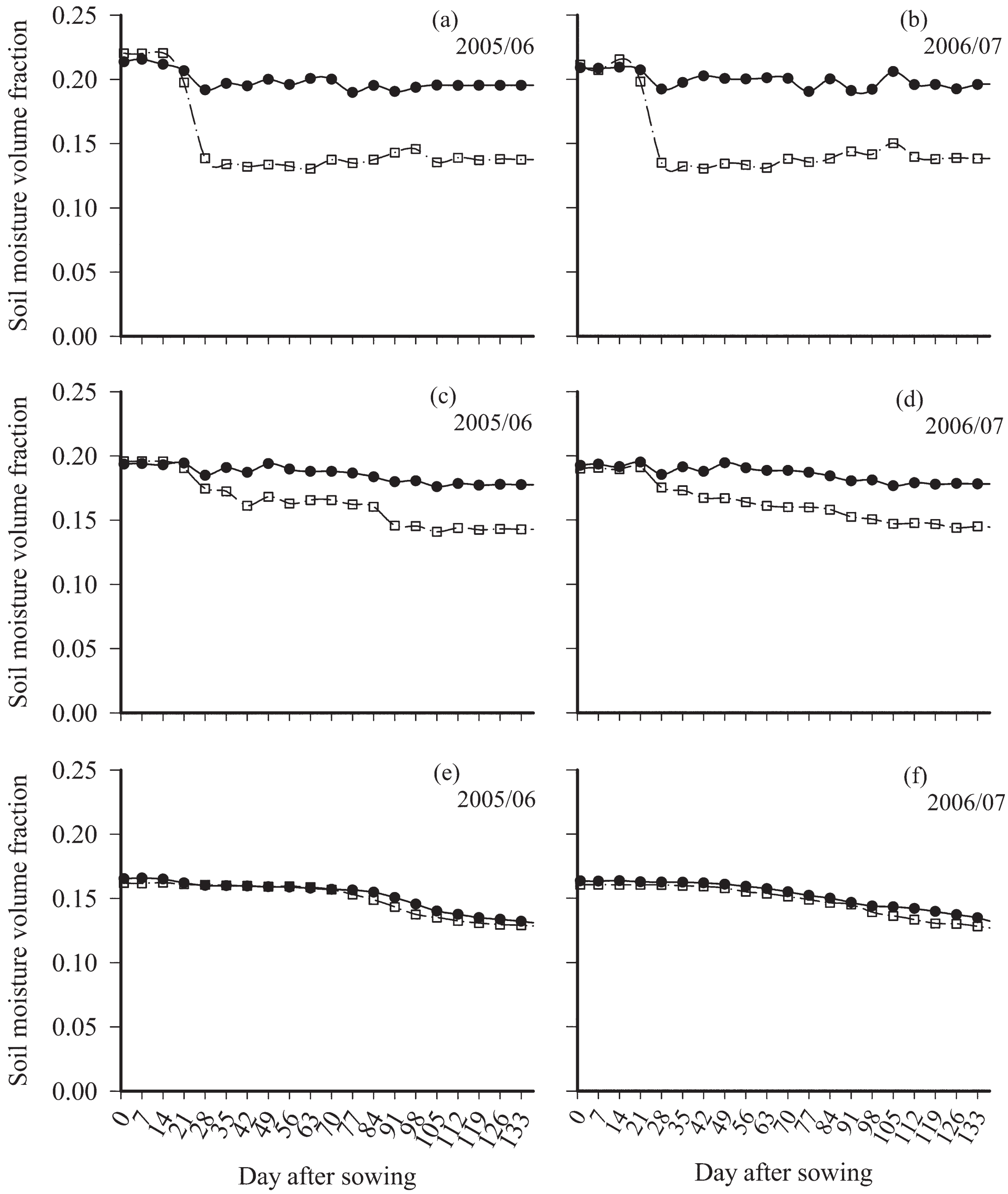

Figure 2. Soil moisture volume fraction in two available soil water regimes [field capacity (FC), ●; and 2/3 available water (AW), □] at (a, b) 30 cm, (c, d) 60 cm, and (e, f) 90 cm of the soil level during the 2005–2006 and 2006–2007 dry seasons in Khon Kaen, Thailand.

Table 2. Mean squares from the combined ANOVA for pod yield, biomass, and drought tolerance index for biomass, DTI (BIO),† and pod yield, DTI (PY), and harvest index (HI) at harvest, SPAD chlorophyll meter reading (SCMR), and specific leaf area (SLA) at 67 d after sowing under nonstressed (Non) and stressed (Stress) conditions of 140 peanut genotypes in the dry season of 2005–2006 and 2006–2007 in Khon Kaen, Thailand.

Source of variation	df	Pod yield			Biomass			HI		SCMR		SLA	
		Non	Stress	DTI (PY)	Non	Stress	DTI (BIO)	Non	Stress	Non	Stress	Non	Stress
Year (Y)	1	19.03	10.57**	0.17	209.41	39.11	0.49	0.00	0.04*	12.58	0.43	969.73	596.56
Rep. within Y	6	3.55	0.52	0.21	40.07	7.27	0.19	0.01	0.01	33.59	38.00	409.12	153.09
Genotypes (G)	139	2.95**	2.17**	0.39**	14.98**	14.60**	0.16**	0.03**	0.02**	57.48**	56.58**	124.53**	89.11**
Y × G	139	0.13**	0.10**	0.03	0.66	1.83	0.04	0.00	0.00*	2.79	2.48	11.68	5.17
Pooled error	834	0.09	0.07	0.03	0.78	1.73	0.04	0.00	0.00	4.08	3.58	14.04	7.77

*Significant at $P \leq 0.05$.

**Significant at $P \leq 0.01$.

†DTIs were calculated by the ratio of stressed (2/3 available water)/nonstressed (field capacity) conditions.

be estimated. The interaction effects of Y × G were significant ($P \leq 0.01$) for pod yield under well-watered and 2/3 AW conditions and significant ($P \leq 0.05$) for HI under 2/3 AW condition. In theory, pod yield is a complex trait in which multiple genes are involved, and high G × E interaction is expected (Wright et al., 1996). Based on low coefficient of variation and high F-ratio from analysis of variance, the best assessment times for SLA and SCMR was determined to be 67 DAS.

Heritability of Drought Resistance Traits

Heritability estimates within four peanut crosses were calculated for SCMR and SLA at 67 DAS, and for HI, DTI (BIO), and DTI (PY) at harvest (Table 3). Heritability estimates for HI, SLA, and SCMR were high for all four peanut crosses under both nonstressed and stressed conditions, ranging from 0.81 to 0.97. Drought tolerance indexes for pod yield and biomass showed lower heritability estimates than those for pod yield and biomass themselves under nonstressed and stressed conditions. Heritability estimates for BIO and PY varied from 0.73 to 0.98, and DTI (BIO) and DTI (PY) varied from 0.54 to 0.96.

Most characters had similar heritability estimates when compared between different water levels. This should make selection for drought tolerance easier. However, DTI is still useful in explaining how some genotypes had higher pod yield under drought. Previous reports on inheritance of drought resistance traits suggested a predominant role of additive gene effects in SLA and HI inheritance (Nigam et al., 2001; Surihan et al., 2005). In early generations (F_3 and F_4), Cruickshank et al. (2004) reported that broad-sense heritability of transpiration, TE, and HI were varied among peanut crosses and traits depending on levels of genetic variation in parents. Information on heritability of drought resistance traits [DTI (BIO), DTI (PY), HI, SCMR, and SLA)] under both stressed and nonstressed are needed for predicting progress from selection. Most of the drought resistance traits in our study had high heritability estimates, indicating that breeding progress could be achieved for these characters.

Table 3. Estimates of heritability with standard error for biomass (BIO), pod yield (PY), drought tolerance index for biomass, DTI† (BIO), and pod yield, DTI (PY), and harvest index (HI) at harvest and specific leaf area (SLA) and SPAD chlorophyll meter reading (SCMR) at 67 d after sowing of four crosses of peanut under stressed and nonstressed conditions in the dry seasons of 2005–2006 and 2006–2007 in Khon Kaen, Thailand.

Cross	Heritability						
	BIO	PY	DTI (BIO)	DTI (PY)	HI	SLA	SCMR
Stressed							
ICGV 98308 × ‘KK60-3’	0.94 ± 0.06	0.93 ± 0.07	0.93 ± 0.07	0.86 ± 0.11	0.94 ± 0.05	0.93 ± 0.07	0.89 ± 0.10
ICGV 98308 × ‘Tainan 9’	0.81 ± 0.16	0.95 ± 0.05	0.54 ± 0.25	0.92 ± 0.07	0.89 ± 0.08	0.81 ± 0.15	0.96 ± 0.03
ICGV 98324 × ‘KK60-3’	0.73 ± 0.20	0.93 ± 0.07	0.67 ± 0.21	0.87 ± 0.11	0.95 ± 0.04	0.91 ± 0.08	0.92 ± 0.08
ICGV 98324 × ‘Tainan 9’	0.96 ± 0.04	0.97 ± 0.03	0.86 ± 0.12	0.96 ± 0.03	0.89 ± 0.08	0.95 ± 0.05	0.96 ± 0.04
Nonstressed							
ICGV 98308 × ‘KK60-3’	0.89 ± 0.12	0.91 ± 0.08	—	—	0.94 ± 0.04	0.83 ± 0.15	0.89 ± 0.11
ICGV 98308 × ‘Tainan 9’	0.98 ± 0.02	0.98 ± 0.02	—	—	0.97 ± 0.02	0.91 ± 0.09	0.97 ± 0.02
ICGV 98324 × ‘KK60-3’	0.93 ± 0.07	0.93 ± 0.06	—	—	0.92 ± 0.06	0.91 ± 0.09	0.90 ± 0.08
ICGV 98324 × ‘Tainan 9’	0.98 ± 0.02	0.98 ± 0.01	—	—	0.96 ± 0.03	0.95 ± 0.05	0.96 ± 0.04

†DTIs were calculated by the ratio of stressed (2/3 available water)/nonstressed (field capacity) conditions.

Genotypic Correlation among Drought Resistance Traits

Phenotypic and genotypic correlations provided similar information in this study, and only genotypic correlations are reported. Strong and negative genotypic correlations were found between SLA and SCMR under both stressed and nonstressed conditions (−0.61, $P \leq 0.01$, and −0.66, $P \leq 0.01$, respectively) (Table 4). In previous studies, the simple correlation between SLA and SCMR was reported under nonstressed conditions (Wright et al., 1994; Nageswara Rao et al., 2001; Upadhyaya, 2005) and end-of-season drought conditions (Nigam and Aruna, 2008). In this study, we evaluated material in both stressed and nonstressed conditions in the same trials. Our finding show that genotypic and phenotypic correlations between SLA and SCMR were consistent under both FC and 2/3 AW conditions. The results show consistency of SLA and SCMR in a wide range of soil water levels and drought conditions. Drought tolerance index for pod yield had strong and positive genotypic correlation with DTI (BIO) (0.69, $P \leq 0.01$). Harvest index was quite low correlated with DTI (PY) under stressed condition (0.37, $P \leq 0.01$) and also was correlated with SCMR both under drought and well-watered conditions (0.13, $P \leq 0.01$, and 0.33, $P \leq 0.01$, respectively).

Genotypic Correlation between Drought Resistance Traits and Yield and Yield Components

Genetic correlations between drought resistance traits and yield and yield components provide information on expected responses in yield and yield components from selection for drought resistance traits. High genotypic correlations were found for HI and PY under drought (0.76, $P \leq 0.01$) and nonstressed (0.79, $P \leq 0.01$) conditions, and for HI with the number of mature pods per plant under both stressed and nonstressed treatments (0.62, $P \leq 0.01$, and 0.49, $P \leq 0.01$, respectively) (Table 5). The genotypic correlations between HI and seed size were also moderate and positive under both stressed and well-watered conditions (0.50, $P \leq 0.01$, and 0.47, $P \leq 0.01$, respectively). The surrogate traits for WUE (SLA and SCMR) (Wright et al., 1994; Nageswara Rao and Wright, 1994; Sheshshayee et al., 2006) had low correlation with pod yield. However, SCMR had higher genotypic correlations with PY, BIO, and other agronomic traits under both stressed and well-watered conditions than did SLA. SCMR showed quite low positive correlations with biomass (0.18; $P \leq 0.01$) and pod yield (0.21; $P \leq 0.01$) under stressed and moderate positive correlations with BIO (0.41; $P \leq 0.01$) and PY(0.51; $P \leq 0.01$) under well-watered conditions. SPAD chlorophyll meter reading was moderate positively correlated with seed size under stressed (0.43, $P \leq 0.01$) and well-watered (0.48; $P \leq 0.01$) conditions. DTI (BIO) and DTI (PY) had moderate positive correlations with biomass (0.47, $P \leq 0.01$, and 0.52, $P \leq 0.01$, respectively), with pod yield (0.34, $P \leq 0.01$, and 0.57, $P \leq 0.01$, respectively), and with number of mature pods per plant (0.34, $P \leq 0.01$, and 0.45, $P \leq 0.01$, respectively) under drought conditions. SPAD chlorophyll meter reading and SLA were strongly and negatively correlated at all evaluation dates (data not shown), and this association was relatively stable across environments (stressed and well-watered).

Among drought resistance traits [DTI (BIO), DTI (PY), HI, SCMR and SLA], HI had the highest correlation with PY, but the measurement of HI was more difficult, laborious, and costly than that of PY. Also, genetic correlations between SCMR and PY and HI were low. However, these traits have lower G × E interaction than do yield (Wright et al., 1996). It would be possible to

Table 4. Genotypic (r_G) correlation estimates among drought resistance traits for all four peanut crosses of 140 genotypes in the dry seasons of 2005–2006 and 2006–2007 in Khon Kaen, Thailand (df = 556).†

	Stressed				Nonstressed		
	DTI‡ (PY)	SCMR	SLA	HI	SCMR	SLA	HI
DTI (BIO)	0.69**	–0.34**	0.05	0.06	—	—	—
DTI (PY)		–0.28**	0.06	0.37**	—	—	—
SCMR			–0.61**	0.13**		–0.66**	0.33**
SLA				0.11*			–0.10*

*Significant at $P \leq 0.05$.

**Significant at $P \leq 0.01$.

†DTI, drought tolerance index; BIO, biomass, PY, pod yield, SCMR, SPAD chlorophyll meter reading; SLA, specific leaf area; HI, harvest index.

‡DTIS were calculated by the ratio of stressed (2/3 available water)/nonstressed (field capacity) conditions.

Table 5. Genotypic (r_G) correlation estimates between drought resistance traits and agronomic traits for all four peanut cross of 140 genotypes in the dry seasons of 2005–2006 and 2006–2007 in Khon Kaen, Thailand (df = 556).†

Drought resistance traits	Agronomic traits				
	BIO	PY	Seed size	No. mature pods/plant	Seed/pod
Stressed					
DTI‡ (BIO)	0.47**	0.34**	0.01	0.34**	0.29**
DTI (PY)	0.52**	0.57**	0.25**	0.45**	0.14**
SCMR	0.18**	0.21**	0.43**	–0.20**	–0.04
SLA	0.07	0.07	0.06	0.04	0.10*
HI	0.19**	0.76**	0.50**	0.62**	0.16**
Nonstressed					
SCMR	0.41**	0.51**	0.48**	0.02	0.24**
SLA	0.01	–0.09*	–0.12**	0.02	0.06
HI	0.01	0.79**	0.47**	0.49**	0.26**

*Significant at $P \leq 0.05$.

**Significant at $P \leq 0.01$.

†DTI, drought tolerance index; BIO, biomass, PY, pod yield, SCMR, SPAD chlorophyll meter reading; SLA, specific leaf area; HI, harvest index.

‡DTI were calculated by the ratio of stressed (2/3 available water)/nonstressed (field capacity) conditions.

improve yield by selecting for high HI and SCMR. The SCMR is an indicator of the photosynthetically active light-transmittance characteristics of the leaf and positive correlated with chlorophyll content (Akkasaeng et al., 2003) and chlorophyll density (Arunyanark et al., 2008) and WUE (Sheshshayee et al., 2006).

Nonetheless, the integration of physiological traits (or their surrogates) in the selection scheme would be advantageous in selecting genotypes that are more efficient water utilizers (SCMR [surrogates trait]) or partitioners of photosynthates into economic yield (HI) (Nigam et al., 2005). The SPAD chlorophyll meter provides an easy opportunity to integrate a surrogate measure of WUE with PY, in the selection scheme of a drought resistance breeding program in peanut.

Relationship of Drought Resistance Traits under Well-Watered versus Drought Conditions

A comparison of drought resistance traits under well-watered versus drought conditions should provided a better understanding of the most suitable conditions for selecting drought resistant genotypes. Significant correlations between traits under stressed and nonstressed conditions were found in all four peanut crosses for HI, SCMR, SLA, PY, and BIO (Table 6), indicating that theses traits could be selected either under well-watered or water-stressed conditions. As heritability estimates were high under both well-watered and stress conditions and the traits under different water regimes were correlated well, it is advisable to first select peanut genotypes under well-watered conditions in large early segregating populations because drought simulation is much more difficult; later, the selections can be refined under both drought and nonstressed conditions in advanced generations.

CONCLUSION

In summary, most traits measured in these four peanut crosses had high heritability, indicating that breeding progress should be possible. The results of the present study indicated that harvest index, SPAD chlorophyll meter reading, and specific leaf area observations can be recorded at both stressed and nonstressed conditions. This gives peanut breeders a large flexibility to record these observations in a large number of segregating populations and breeding lines in the field, thus making it easy to incorporate these physiological traits associated with drought tolerance in breeding and selection schemes in peanut. SPAD chlorophyll meter reading should be particularly useful as a selection criterion for drought tolerance in peanut because of high heritability and the simplicity in gathering.

Table 6. Correlation coefficients of biomass (BIO), pod yield (PY), harvest index (HI), specific leaf area (SLA), and SPAD chlorophyll meter reading (SCMR) of four peanut crosses under stressed (d) and well-watered (w) conditions during 2005–2006 and 2006–2007 in Khon Kaen, Thailand (df = 33).

Correlation	Peanut cross			
	ICGV 98308 × ‘KK60-3’	ICGV 98308 × ‘Tainan 9’	ICGV 98324 × ‘KK60-3’	ICGV 98324 × ‘Tainan 9’
BIO_w vs. BIO_d	0.48**	0.79**	0.62**	0.84**
PY_w vs. PY_d	0.35*	0.73**	0.61**	0.71**
HI_w vs. HI_d	0.75**	0.62**	0.58**	0.46**
$SCMR_w$ vs. $SCMR_d$	0.73**	0.84**	0.53**	0.86**
SLA_w vs. SLA_d	0.59**	0.35*	0.52**	0.86**

*Significant at $P \leq 0.05$.

**Significant at $P \leq 0.01$.

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References

Akkasaeng, C., N. Vorasoot, S. Jogloy, and A. Patanotai. 2003. Relationship between SPAD readings and chlorophyll contents in leaves of peanut (*Arachis hypogaea* L.). Thai J. Agric. Sci. 36(3):279–284.

Arunyanark, A., S. Jogloy, C. Akkasaeng, N. Vorasoot, T. Kesmala, R.C. Nageswara Rao, G.C. Wright, and A. Patanothai. 2008. Chlorophyll stability is an indicator of drought tolerance in peanut. J. Agron. Crop Sci. 194:113–125.

Boote, K.J. 1982. Growth stage of peanut (*Arachis hypogaea* L.). Peanut Sci. 9:35–40.

Bricker, A.A. 1989. MSTAT-C user’s guide. Michigan State Univ., East Lansing.

Cruickshank, A., A. Dowkiw, G.C. Wright, C.R. Nageswara Rao, and S.N. Nigam. 2004. Heritability of drought–resistance traits in peanut. *In* T. Fischer, N. Turner, J. Angus, L. McIntyre, M. Robertson, A. Borrell, D. Lloyd (ed.) New directions for a diverse planet: Proceedings for the 4th Int. Crop Science Congress, Brisbane, Australia. 26 Sept.–1 Oct. 2004.

Doorenbos, J., and A.H. Kassam. 1986. Groundnut. p. 97–100. *In* Yield response to water. FAO Irrigation and Drainage Paper 33. FAO, Rome.

Doorenbos, J., and W.O. Pruitt. 1992. Calculation of crop water requirements. p. 1–65. *In* Guidelines for predicting crop water requirements. FAO Irrigation and Drainage Paper 24. FAO, Rome.

Falconer, D.S., and T.F.C. Mackay. 1996. Introduction to quantitative genetics. 4th ed. Longman, London.

Farquhar, G.D., M.H. O’Leary, and J.A. Berry. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Aust. J. Plant Physiol. 9:121–137.

Gomez, K.A., and A.A. Gomez. 1984. Statistical procedures for agricultural research. 2nd ed. John Wiley & Sons, New York.

Holland, J.B. 2001. Epistasis and plant breeding. Plant Breed. Rev. 21:27–92.

Holland, J.B., W.E. Nyquist, and C.T. Cervartes-Martinez. 2003. Estimating and interpreting heritability for plant breeding: An update. Plant Breed. Rev. 22:2–112.

Hubick, K.T., G.D. Farquhar, and R. Shorter. 1986. Correlation between water-use efficiency and carbon isotope discrimination in diverse peanut (*Arachis*) germplasm. Aust. J. Plant Physiol. 13:803–816.

Nageswara Rao, R.C., H.S. Talwar, and G.C. Wright. 2001. Rapid assessment of specific leaf area and leaf nitrogen in peanut (*Arachis hypogaea* L.) using a chlorophyll meter. J. Agron. Crop Sci. 186:175–182.

Nageswara Rao, R.C., M. Udaykumar, G.D. Farquhar, H.S. Talwar, and T.G. Prasad. 1995. Variation in carbon isotope discrimination and its relationship to specific leaf area and ribulose–1, 5–bisphosphate carboxylase content in groundnut genotypes. Aust. J. Plant Physiol. 22:545–551.

Nageswara Rao, R.C., and G.C. Wright. 1994. Stability of the relationship between specific leaf area and carbon isotope discrimination across environments in peanut. Crop Sci. 34:98–103.

Nautiyal, P.C., R.C. Nageswara Rao, and Y.C. Joshi. 2002. Moisture-deficit–induced changes in leaf water content, leaf carbon exchange rate and biomass production in groundnut cultivars differing in specific leaf area. Field Crops Res. 74:67–79.

Nigam, S. N., and R. Aruna. 2008. Stability of soil plant analytical development (SPAD) chlorophyll meter reading (SCMR) and specific leaf area (SLA) and their association across varying soil moisture stress conditions in groundnut (*Arachis hypogaea* L.). Euphytica 160:111–117.

Nigam, S.N., H.D. Upadhyaya, S. Chandra, R.C. Nageswara Rao, G.C. Wright, and A.G.S. Reddy. 2001. Gene effects for specific leaf area and harvest index in three crosses of groundnut (*Arachis hypogaea*). Ann. Appl. Biol. 139:301–306.

Nigam, S.N., S. Chandra, K. Rupa Sridevi, A. Manoha Bhukta, G.S. Reddy, R.C. Nageswara Rao, G.C. Wright, P.V. Reddy, M.P. Deshmukh, R.K. Mathur, M.S. Basu, S. Vasundhara, P. Vindhiya Varman, and A.K. Nagda. 2005. Efficiency of physiological trait-based and empirical selection approaches for drought tolerance in groundnut. Ann. Appl. Biol. 146:433–439.

Passioura, J.B. 1986. Resistance to drought and salinity: Avenues for improvement. Aust. J. Plant Physiol. 13:191–201.

Reddy, T.Y., V.R. Reddy, and V. Anbumozhi. 2003. Physiological responses of peanut (*Arachis hypogaea* L.) to drought stress and its amelioration: A critical review. Plant Growth Regul. 41:75–88.

Sheshshayee, M.S., H. Bindumadhava, N.R. Rachaputi, T.G. Prasad, M. Udayakumar, G.C. Wright, and S.N. Nigam. 2006. Leaf chlorophyll concentration relates to transpiration efficiency in peanut. Ann. Appl. Biol. 148:7–15.

Singh, S., and M.B. Russell. 1981. Water use by maize/pigeonpea intercrop on a deep Vertisol. p. 271–282. *In* Proc. Int. Workshop on Pigeonpeas. 15–19 Dec 1980. Vol. 1. ICRISAT Cente. Patancheru, AP, India.

Singh, M., S. Ceccarelli, and J. Hamblin. 1993. Estimation of heritability from varietal trials data. Theor. Appl. Genet. 86:437–441.

Surihan, B., A. Patanothai, and S. Jogloy. 2005. Gene effect for specific leaf area and harvest index in peanut (*Arachis hypogaea* L.). Asian J. Plant Sci. 4(6):667–672.

Upadhyaya, H.D. 2005. Variability for drought resistance related traits in the mini core collection of peanut. Crop Sci. 45:1432–1440.

Wright, G.C., K.T. Hubick, and G.D. Farquhar. 1988. Discrimination in carbon isotopes of leaves correlates with water-use efficiency of field-grown peanut cultivars. Aust. J. Plant Physiol. 15:815–825.

Wright, G.C., and R.C. Nageswara Rao. 1994. Peanut water relations. p. 281–325. *In* J. Smartt (ed.) The groundnut crop. Chapman & Hall, London.

Wright, G.C., R.C. Nageswara Rao, and M.S. Basu. 1996. A physiological approach to the understanding of genotype by environment interactions: A case study on improvement of drought adaptation in groundnut. p. 365–380. *In* M. Cooper and G.L. Hammer (ed.) Plant adaptation and crop improvement. CAB Int., Wallingford, UK.

Wright, G.C., R.C. Nageswara Rao, and G.D. Farquhar. 1994. Water use efficiency and carbon isotope discrimination in peanut under water deficit conditions. Crop Sci. 34:92–97.